MIGRATION AND EVOLUTION IN PLANTS[1]

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It will be my objective to point out that the dynamics of the genetic elaboration of the plant population over the available habitats is the dynamics of natural selection and that genetic variation and natural selection together provide the dynamics of plant migration. Hence, plant migration and the organic evolution of each genetic lineage involved are concomitant.

The Concept of Migration

There are at least three different types of movement of natural populations, each of which may be spoken of as migration. There is the oscillating phenomenon such as the back and forth movement of ducks and geese wherein these animals migrate closely in tune with the seasonal progression of climate. This we may speak of simply as *seasonal migration.* Although these animals are adapted genetically to this mode of life, the dynamics of seasonal migration do not involve the simultaneous and obligate genetic elaboration of the population over area.

A second type of migration is the impulsive or sporadic movement of organisms possibly related to overpopulation phenomena. Here we have such phenomena as the curious suicidal migrations of the arctic lemming and the occasional mass migrations of excessively large populations of rodents such as the migration of mice in the San Joaquin Valley of California a few years ago. Such *sporadic migrations* do not necessarily involve the genetic elaboration of the population, although with the increase in density of the population there is probably a concomitant increase in its genetic variability.

A third type of migration is not seasonally oscillatory, but it may at times appear as though sporadic. It is often persistently directional through long time, and always involves the lineal succession of individuals. It may be either a response to secular environmental changes or to the local environmental selection of fortuitous adaptive changes that are products of genetic variation. More commonly, these changes operate together. Because such changes usually include occurrences on a scale of very long time periods even in terms of geological time, we may speak of this type of migration as *secular migration.*

Both seasonal and sporadic migration are known only in animals. Secular migration may occur in both animals and plants. For instance we have fossil evidence that both the camel and the horse originated in North America, where they are now extinct, and migrated to the old world, where they still persist in the form of changed modern descendants. We have

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similar evidence of the migration of plants which we are able to trace through the "flashes" of the fossil record and through which we may interpret the evolutionary changes that have taken place during this migration.

The important difference between secular migration and seasonal and sporadic migration is that secular migration, because it is involved with the linear reproductive succession of individuals through time, is obligately concerned with the genetic elaboration of the population over environments. Such genetic elaboration of the population over environments is a significant part of the migrational dynamics. This need not be the case with either seasonal or sporadic migration.

It is necessary that I make clear that migration and dispersal are not synonymous. Dispersal is the movement of an organism in any form from one place to another (Ridley, 1930). If, however, after dispersal, the individual is unable to survive and reproduce, there is no migration (Clements, 1916). At any given time with any species population the potential scope of dispersal is infinitely greater than is the potential scope of migration. Seeds regularly find their way into many habitats in which there is no chance of their survival. Perhaps the best examples are the hundreds of cultivated plants dispersed by man through cultivation which are unable to survive in the areas into which they are introduced except through the care given them by man. Assuming that activities associated with man's culture are artificial, such introduced plants are not regarded as part of the natural plant population. On the other hand, many of our weeds, dispersed through man's carelessness, became established and now are self-perpetuating populations. These are examples of effective steps in migration.

Dispersal beyond the habitat of the population provides that genetic variants, initiated in the population, may reach a new environment to which they may be adapted and by which they may be selected for survival. If the new area is contiguous to the old, the area of the population is extended, and the survival of the new variant may, through gene exchange, serve to stimulate the pattern of genetic variability of the population as a whole. If the new area is not contiguous a new, isolated or semi-isolated race is established.

It is also important that I point out that we have traditionally thought of secular migration in terms of the migration of floras and faunas (Chaney, 1936). Such apparent mass migrations are strictly coincidental insofar as dynamics are concerned. If we are to study and interpret migrations in terms of dynamics we must concern ourselves solely with the activities of successive individuals within interbreeding populations functioning under the influence of environmental conditions.

The Dynamics of Migration

In a previous paper (Mason, 1946) I have pointed out that there are three aspects to the scope of the dynamics of any problem in plant geography. First, there is the individual organism carrying on the vital processes that insure its survival and provide for the continuity of the population. These vital processes are physiological in scope and they operate in accordance with the theory of physiological limits and the principle of limiting factors, and they are influenced by the conditions of the environment. Secondly, there is the genetics of the population which is concerned with the actual gene exchange between individuals and the genic changes that may result from any of the mutagenic agencies that may operate in the populations. These may set the physiological capacity of the individual with respect to its various functions. Thirdly, there is the environment as it varies over area and through time. The conditions of the environment may function as barriers to migration or they may serve as migration lanes. Through environmental control over physiological function the environment selects its plant population. This is, in effect, natural selection.

THE PHYSIOLOGY OF THE INDIVIDUAL. The functioning of plants is conditioned by the factors of the environment as they operate to control physiological processes. The relationship between environment and precise physiological process is probably genetically fixed within each individual plant as to the nature of the span of tolerance of the particular environmental factors concerned. The fixation of the tolerance span may result from any of the gene assorting and gene modifying mechanisms of cytology and genetics as these operate to allocate a given set of genic materials to each individual plant. Physiological characters, as imparted by gene combinations, vary among the individuals of the population in the same way that morphological characters do. They might and probably do vary to the extent that many of the seeds produced are incapable of functioning under the environmental regime in any of the available habitats. However, they could function in some other habitat should chance dispersal enable the seed to reach that habitat.

It is especially important to our thesis that we emphasize the role of variation in physiological capacity of individuals of a population. The vital physiological processes that go on within each individual plant operate within the basic structure of the theory of tolerance and the principle of limiting environmental factors. It is because of this that there is a close relationship between the plant and the environment. It is because of the variation in physiological capacity and the role of limiting environmental factors that different kinds of plants occur in different kinds of habitats. We can speak broadly and say that some kinds of plants grow only in the tropics while others grow only in the arctics. Or, as research in this field advances, we can speak in increasingly precise terms. We now know that species become elaborated over area in direct proportion to their genetic diversity with respect to physiological characters on the one hand and, on the other, to the degree that these variants become dispersed into suitable habitats. The experimental work of Clausen, Keck and Hiesey (1948) on *Achillea* gives ample evidence of this. Thus, individuals comprising a species may be aggregated into populations that differ from one another to a greater or lesser degree. Today, facts discovered during the research of some of my students enable us to carry this even further. We may now state that the precise distributional pattern, even within some small interbreeding populations, reflects a pattern of genetic diversity in the physiological capacity of the individuals that have been selected by a pattern of local habitat variation. Some members of the same interbreeding population can survive through selection in one part of the area of the population, but would be rejected and perish in another part of the area of this same small population. It is because the physiological processes of plants operate within limits or extremes of environmental conditions that they are important in determining the area in which species can live. Since the range of tolerance is subject to the laws of evolution and genetics and is as characteristic of the plant as are its morphological characters, it is to be expected that there will be variation from one individual to another within the interbreeding population. Variation in tolerances thereby becomes the basis of explaining how the members of a species become elaborated over a complex set of environmental conditions, the total range of which is beyond the capacity of any one individual. Each individual is but an increment in the total range of the species. One individual may extend the tolerance of the species population in the direction of one environmental extreme while another individual will extend it in the direction of another extreme.

Thus the physiological processes of the plant, whether they involve nutrition, respiration, growth, or reproduction operate under the influence or sanction of the environmental conditions. The environmental condition circumscribes the area in which the function can operate. Variation in physiological capacity among individuals almost certainly demands that the plants will occupy different kinds of habitats.

The Genetics of Individuals in Populations. The interbreeding population, through the physiological functioning of individuals and the mechanism of gene exchange, sets up a self-perpetuating dynamic system so that functioning individuals continually are being produced as old ones die. Because there are always individuals present, the population is said to persist. Persistence of the population and of the species is thus vested in the reproductive process of individuals of the population. For the most part, these processes are sexual processes which, because of their attendant cytological phenomena, set in motion the mechanics of population genetics. Persistence of the population is not guaranteed through population genetice, but no better device has as yet been produced to insure opportunity for survival in the face of fluctuating and changing environmental conditions. In meeting these situations, some populations have both migrated and undergone evolutionary changes. Other populations have not been genetically adaptable and have perished. I have previously pointed out (Mason, 1946) that genetics, by whatever mechanism it may operate, in each individual case functions to set the capacity of the plant to tolerate the conditions of the environment. Once the zygote is formed, the potential individual will be capable of carrying on all of its vital functions only under the environmental conditions to which it may be thus preadapted. Usually seed grow only in an environment similar to that in which the parents grew, but genetic processes may result in production of seed having somewhat different capacities than those of the parents, capacities that enable the progeny to become established and survive in slightly different or new environments. Such new environments have nothing to do with the *preadaptation* of these seeds that become established there. They can only select or reject an already adapted individual. The role of genetics, so far as the potential characters of this individual are concerned, is ended with the formation of the zygote. Since reproductive processes continue in the population, we may think of the population as thereby being continuous beyond the life span of any single individual member. The continuity in reality is the many successions of individuals, overlapping in their duration.

That the relation between function and conditioning environmental factors is genetically fixed within each individual plant has been established through considerable research (Turesson, 1922; Clausen, Keck and Hiesey, 1940, 1948). However, no individual represents the total span of variation exhibited by the population as a whole. Breeding programs for earliness or lateness in agricultural crops in local situations are dealing essentially with the genetics of physiological characters. The fixing of the tolerance spans within individuals may result from any of the mechanisms operating in genetics which function to apportion gene materials among gametes.

Out of the mass of preadapted seed received, the environment permits the survival of only those which are capable of carrying on all of their vital functions under the conditions prevailing in that environment. This repeated selection, generation after generation, tends to fix the form and the physiological capacity of the mass of individuals that constitute the species population in that environment, and it tends to control the range of genetic variation within the species population. Thus any mutant in the population which has the potentiality of affecting physiological relations will soon be eliminated should it produce an effect that is not selected by the environment. On the other hand, should the mutant produce a better relationship with the environment, or should it enable the population to expand its area into new habitats, it will be favored and will tend to increase the genetic diversity of the population and thus increase the survival chances of the population in the face of environmental fluctuation and change. This is essentially the mechanism of natural selection.

Thus the genotypes within the species population become modified by environmental selection. This is what Turesson (1922) called, "genotypical response of the plant species to the habitat." Such selection results locally in a genetic race thoroughly in adjustment with its environment. It involves the pattern of interaction between the various factors of the environment, the physiological processes of the plant concerned with germination and establishment and the various functions of individuals.

It is through these processes that the species is able to persist in a given environment through normal fluctuations of environmental conditions. Likewise it is through these genetic processes that variation develops, thus enabling the species to extend itself into new habitats. Only in this way can a migrating plant species overcome the diverse environmental conditions that it would encounter in its migration. Only in this way can we explain the habitat diversity between the species of a genus. In recognizing the role of genetics in plant migration, it is important to reemphasize the point that the seed destined to survive in a new environment arrived in that environment already adapted. Also it is important that we realize that the new environment played no part in this preadaptation. All of this happened through those genetic phenomena that are inherent in the reproductive process under the influence of the environmental relations of the parents.

The Nature of Environment and Environmental Relations. The medium in which the plant grows, involves chiefly the climate and the soils, but it may also include the direct and indirect effects of other organisms. The interaction of climate, soils, and organisms is very complex.

Climatic factors in any given region function within a general pattern of diurnal and seasonal rhythm, such as the daily fluctuations of temperature, or as temperature and rainfall follow a seasonal sequence, or as length of day and length of growing season follow a rhythmic sequence. Often these rhythmic sequences impose a rhythmic sequence on other environmental factors such as the position of the water table, or the salinity of lakes in seasonally arid regions. The nature of such sequential events may be limiting factors to some species of plants. Climatic factors usually occur over area as directional gradients of intensity or amount and no sharp boundaries exist. Where these appear to exist they are usually evidence of a local steepening of the gradient. The nature of these gradients in their effect upon plant populations often becomes selective locally to produce clines within the population with respect to the tolerance of these conditions. Each local race is adapted to the local area of the gradient. This is often evident in the gradient of length of season on the slopes of a mountain of sufficient height where a species occurs throughout. Those plants at low altitudes will be adapted to a long season while those at high altitudes will be adapted to a short season.

Edaphic factors are those pertaining to soil composition and condition. They operate within a situation imposed by local climate and to some extent they may be a product of that local climate. They may be relatively persistent features, expressible in terms of presence; they may vary locally in their intensity or amount; they may fluctuate as a result of chance climatic, biotic or diastrophic events; or they may follow a rhythmic pattern in tune with the rhythm of climate. The edaphic situation often has persistent features of large area such as may be determined by lithologic conditions, or by the position of the water table. Such features in turn produce effects upon soils to which they contribute. In conjunction with local climate, soils may be significantly altered and characterized by accumulations of salts at the surface. There are many ways in which edaphic situations may vary either within themselves or through their interactions with other environmental conditions. In any event, the areas occupied by given sets of edaphic conditions constitute the areas available to plants, and the mosaic of edaphic factors across area provides a significant set of variants for the operation of selection.

Biotic factors present many interpretational problems because the organism itself is subject to climatic and edaphic situations. Furthermore biotic effects may be either direct or indirect. When the influence of an organism is indirect, the organism creates a condition in another factor to which a second organism reacts. For instance a rodent may loosen the soil. The reaction of any plant that might be affected is to the loosened soil rather than to the rodent directly. Loosened soil due to other causes might produce the same effect in the plant.

It should be made clear that because they are often interrelated the problems of environmental factors and their conditioning effects are not simple. They are not solely matters of presence or absence of fluctuating intensities and demands, nor are they the simple problems of gradients between extremes. They may involve coincidences between two or more rhythmic cycles of fluctuating conditions, or fluctuating physiological demands, or of rhythmic sequences in the ontogeny of the plant. Often they serve to condition one another and in so doing, they may alter the physiological response.

When we consider all aspects of the environment, it becomes clear that much of its significance to our problem is the fact that environmental condition occupies area independently of whether or not the precise condition or combination of conditions may influence a particular organism. Thus area is subordinate to environmental condition in determining where a given species can grow. Of equal significance is the fact that environmental condition varies enormously over area, thus presenting a mosaic of conditions sometimes locally rather uniform, sometimes locally very complex. Each such local habitat is either the potential habitat of some chance genetic race of the species population, or it may present a barrier too great for a genetic race to cross by occupancy and successive seed dispersal.

It should be clear that environmental conditions as they occupy area present problems to any migrating species. The magnitude of some of these areas is such as to make it mandatory that the species cross by occupying the area. One individual seed may, by preadaptation and fortuitous dispersal, reach a suitable habitat in the area and become established. Before a second step can be taken normally, the reproductive process must take place to produce additional migrules. These, if they succeed, build a local interbreeding population.

In the process of migration, environmental diversity must be met and overcome through the development of individuals and races of the species population preadapted to the new environmental situations that are encountered in the migration. Although in general the population must cross such areas by inhabiting them, some fortuitous long-jump dispersal may at times occur. The greater the genetic diversity of the population, the greater are its chances of survival in the face of the hazards of migration. A genetically stable species has little chance of success as a migrant. We must bear in mind that migration is possible through successive genotypic changes which meet the pattern of the environment encountered. Climatic change usually makes it mandatory that the species population either migrate, become adapted to the change, or perish. Under conditions of climatic change, the species population may remain within range of the same climatic conditions by migrating in pace with the change. In so doing, however, it encounters very great edaphic diversity to which it must become accommodated or it will perish. Such a migrating population may leave behind descendant populations capable of adjustment to further climatic changes. These populations may become points of origin of further evolutionary diversification.

In conclusion, we may say that simultaneous with migration we usually find evolutionary diversification by means of genetic elaboration of the migrating lineages. Thus, the population is accommodated to the environmental diversity that it encounters. The interbreeding population provides the necessary reservoir of genic materials for recombination in varying manner. It thereby provides for the persistence of the species through adjustment to environmental fluctuation and change and for extending the area through genetic change. At length these changes may be of profound scope and be spoken of as evolution.

It is doubtful if any extensive long-term migration is possible without significant evolutionary change in physiological capacity. It seems probable that only plants undergoing active speciation are capable of extensive migration. It would seem therefore that an elaborate taxonomic and geographic pattern in any group of plants would stand as testimony of a former highly vigorous genetic nature.

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CHROMOSOME NUMBERS, APOMIXIS, AND INTERSPECIFIC HYBRIDIZATION IN THE GENUS TOWNSENDIA[1]

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The genus *Townsendia* Hooker, of the tribe Astereae of the Compositae, consists of about twenty species of small annual, biennial, or perennial, western North American plants. The genus was revised by Larsen (1927), but since that time several poorly understood taxonomic complexes have become apparent. Since no chromosome studies on any member of the genus had previously been reported, a cytotaxonomic study was initiated in an attempt to solve some of these problems through a better understanding of natural relationships within the genus.

As the study progressed, other problems, chiefly involving apomixis and polyploidy, were encountered. With the appearance of these complications came the realization that *Townsendia* is ideally suited for intensive studies directed toward a further understanding of the roles of hybridization, apomixis, and polyploidy in speciation. The genus has a relatively small number of species and a fairly limited range. Most species flower profusely and can be grown without difficulty in the greenhouse or garden. These advantages make it a convenient subject for experimental studies on some of the mechanics of evolution.

MATERIAL AND METHODS

The collections studied are listed by species in Table 1. Culture number, chromosome number, and source of collection are given. Voucher specimens are filed in the Herbarium of the State College of Washington.

The collections were grown in the greenhouse and most of them also in the experimental garden at Pullman, Washington. Seeds were germinated on moist filter paper in petri dishes, the young seedlings transferred to pots, and some of them later transplanted to the garden. Plants of some collections were transplanted from their natural habitat to the greenhouse

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